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BIOMASS ALLOCATION PATTERNS, AND
NITROGEN USE EFFICIENCY OF LODGEPOLE
PINE IN FORESTS DIFFERING IN DENSITIES AND
AGES OF THE GREATER YELLOWSTONE
ECOSYSTEM

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FINAL REPORT

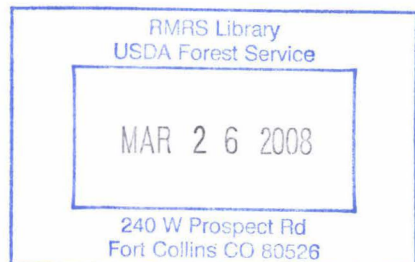
Allometric model development, biomass allocation patterns, and nitrogen use efficiency of lodgepole pine in forests differing in densities and ages of the Greater Yellowstone Ecosystem

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INTRODUCTION

Natural and anthropogenic effects on climatic patterns in the western U.S. are likely to cause substantial changes in natural fire regimes that could result in alterations to forest stand structure and productivity (Amiro et al. 2000). These alterations produce heterogeneity in stand ages and densities (Dale et al. 2001), and this heterogeneity results in wide variability of Net Ecosystem Production (NEP) (Chapin et al. 2002; Turner et al. 2004). For example, in the Greater Yellowstone Ecosystem (GYE), recent and historic fires have created a complex mosaic of varying forest stand structures (Turner et al. 1997). Understanding the variability in NEP is, at least in part, dependent upon knowledge of how individual trees allocate biomass in response to such differences in forest structure. Quantification of forest structure and function requires accurate and easily obtained measurements of above and belowground tree biomass, which are necessary components for determining Net Primary Production (NPP), a major component of NEP in forested ecosystems.

Lodgepole pine (*Pinus contorta* var. *latifolia* (Engelm. ex Wats.) Critchfield) dominates the forested plateaus of the GYE (Tinker et al. 1994), and therefore contributes greatly to the NEP of the ecosystem. The successional pathways of stand development for lodgepole pine vary widely after disturbances such as fire, where initial seedling densities may range from < 100 to > 500,000 seedlings/ha (Turner et al. 2004). As the forests mature, this heterogeneous landscape is somewhat homogenized by a convergence in stand density (Kashian et al. 2005), resulting in considerable variability in spatial and temporal patterns of biomass accumulation and net primary production (NPP) across the landscape (Litton et al. 2004) (Turner et al. 2004). Estimating the biomass of these vast forests is a critical component in determining the NPP of lodgepole forests across the entire Greater Yellowstone Ecosystem (GYE).

Useful allometric equations for above and belowground biomass of lodgepole pine have been developed in Alberta, Canada by Johnstone (1971), in southeastern WY by Pearson et al. (1984), in southeastern British Columbia by Comeau and Kimmins (1989), and in Washington and Oregon by Gholz et al. (1979). More recently, allometric equations for predicting biomass in ≈ 10 year-old post-fire forests have also been developed in Yellowstone National Park (YNP) for aboveground biomass by Turner et al. (2004), and for belowground biomass by Litton et al. (2003). Although Litton et al. (2004) later suggested that allometric models developed by Comeau and Kimmins (1989) and Pearson et al. (1984) could be appropriate for use in the GYE, the models were tested on only five mature trees in a single stand, and did not account for natural variability in stand density and age. In addition, allometric models for predicting belowground biomass were not critically evaluated. Therefore, new allometric models specific to mature forests of the Greater Yellowstone Ecosystem are needed. In this study, we developed new allometric models for predicting above and belowground biomass in mature lodgepole pine forests of the GYE.

Recently, allometric models were developed and applied to predict aboveground NPP of young post-fire forests across the entire Yellowstone landscape by Turner et al. (2004). Their landscape scale extrapolation was made possible by the applicability and accuracy of their allometric models. Allometric equations developed for lodgepole pine and many other species (Ter-Mikaelian and Korzukhin 1997) have proven to adequately predict above and belowground biomass for individual trees, where coefficients of determination are often above 0.90 for aboveground tree components and for roots >10 mm diameter. Despite the high quality of allometric equations, previous studies have suggested that they may not be universally applicable in stands of varying densities, ages, and site qualities. Johnstone (1971) identified a need to

consider stand density and age when he developed allometric models for 100-year-old lodgepole pine in Alberta, Canada. Since that study, Pearson et al. (1984) suggested that differences in stand density, age, and site quality may have caused considerable variability in tree crown biomass, and both Pearson et al. (1984), and Comeau and Kimmins (1989) found that the foliage biomass: sapwood area ratio decreased with increasing stand density. Variability among sites suggests that allometrics are also likely to differ among geographic locations due to differences in substrate, topography, and climate. Keyes and Grier (1981) found that Douglas-fir had proportionately more total root biomass on a low productivity site than on a high productivity site, and Comeau and Kimmins (1989) found that belowground production represented a greater proportion of total production in two xeric sites compared to two mesic sites. Therefore, changes in allocation of biomass with differing site productivities may cause changes in allometric relationships across gradients in site productivity that could be caused by differences in substrate, topography, and climate. To accurately estimate NPP, it is important to use allometric equations that consider differences in allocation patterns of lodgepole pine biomass, which may vary with tree density and stand age.

The specific objectives of this study were to: (1) develop allometric models for predicting above and belowground biomass of mature lodgepole pine trees in the GYE; (2) determine how allometric model development and application for lodgepole pine differs with stand density and age; and (3) compare and contrast allometric equations developed in this study to allometric equations developed in other locations to determine model variability and applicability across geographic locations independent of forest structure; (4) to determine how patterns of above and belowground biomass allocation for mature lodgepole pine forest of the GYE vary with stand

age and density; and (5) to estimate the carbon storage in three mature lodgepole pine stands differing in density and age of the Greater Yellowstone Ecosystem.

We hypothesized that allometric models developed for estimating biomass of above and belowground tree components in the GYE would vary with stand density and age, and that allometric models developed for lodgepole pine in the GYE will differ from models developed elsewhere due to differences in substrate, topography, and climatic conditions.

METHODS

Study Area

The study area was located within the GYE on the Caribou-Targhee National Forest (CTNF) bordering YNP. The GYE encompasses portions of three states in the western US: Wyoming, Idaho, and Montana, and is centered around YNP and its surrounding mountains, valleys, and subalpine plateaus. Elevations in YNP range from 1,620 m near Gardiner, Montana to 3,333 m in the Absaroka mountain range of Wyoming. Mean annual precipitation ranges from less than 28 cm yr⁻¹ at lower elevations to about 180 cm yr⁻¹ on the southwestern plateau (Knight 1994). Temperatures are cold during the winter, where high temperatures less than 0°C occur for an average of 87.6 days year⁻¹, and temperatures are rarely more than 32°C during the summer (Dirks and Martner 1982).

There are three main substrates for soil development on the subalpine plateaus of the ecosystem: the least fertile rhyolite; the less infertile rhyolite; and lake bottom sediments (Despain 1990). The dominant forest type of the ecosystem is lodgepole pine forest, which occurs at middle elevations. Spruce/ Fir (*Picea engelmannii* /*Abies lasiocarpa*) forests occur at higher elevations and Douglas-fir (*Pseudotsuga menziesii*) forests occur at lower elevations. Whitebark pine (*Pinus albicaulis*) dominates at the upper treeline and sagebrush (*Artemisia* sp.)

occurs at the lower treeline. Aspen (*Populus tremuloides*) occurs more commonly within the ecosystem outside of YNP (Knight 1994).

Field and Lab Methods

Allometric equations were developed in three lodgepole pine stands on the CTNF that represented two age classes and two density classes (Table 1). In the young (64 years old) age class, two stands of different densities were examined; one dense (YD) (2,452 trees/ha) and the other sparse (YS) (725 trees ha⁻¹). The two young stands were located within the CTNF near Island Park, ID. Because densities of lodgepole pine stands tend to converge as they get older (Kashian et al. 2005), a single sparse (674 trees ha⁻¹) stand was sampled in the older age class (OS) (164 years old).

Although sites differed in density and age, they were located on similar soils. The Koffgo soil series consists of loamy-skeletal, mixed, superactive Vitrandic Cryochrepts. Parent material was local residuum, colluvium, or alluvium developed from volcanic ash, igneous rocks, and loess (Bowerman et al. 1999). Elevations ranged from 1951m to 2249m, which is within the elevation range of lodgepole pine found for the GYE. Precipitation was approximately 114.3 cm yr⁻¹ in the oldest stand and approximately 76.2 cm yr⁻¹ in the younger stands (Dirks and Martner 1982). All sites were located at least 50 m from the road to facilitate equipment hauling and to avoid road influences. Stand basal area was similar between the OS (16.84 m² ha⁻¹) and YS stands (19.71 m² ha⁻¹), but was quite different for the YD stand (28.32 m² ha⁻¹) (Table 1).

All aboveground tree biomass for a total of 46 trees was harvested within the three stands, and 24 root systems were excavated to develop allometric equations where easily obtained morphological parameters, such as diameter at breast height, were tested as predictors of above and belowground tree components (foliage biomass, coarse root biomass, etc.).

Fourteen trees were harvested in the YD stand and 15 trees were harvested in the YS stand; 17 were harvested in the OS stand. For belowground components, 5 root systems were excavated in both the YS and OS stands due to logistical difficulties associated with large root systems, while 14 root systems were harvested in the YD stand. Initially, we decided to harvest 15 trees in each stand. However, in the OS stand, three extra trees were harvested to ensure that all trees were within the proper age range, and one tree had to be removed because it was younger than the acceptable age range (150-165 years) for that stand. In addition, some field data for one tree in the YD stand was missing, and therefore, that tree was not included in the analyses.

Five trees were harvested along each of three 25m transects in each stand. Trees were generally selected at 5m intervals along each transect, but more importantly, trees were selected based on their diameter to represent the range of tree sizes found for trees in their respective stands. Trees were not chosen if they had any of the following characteristics: unusually poor tree form, such as crook or sweep of the bole; major forking of the bole; excessive mistletoe; any defect that would alter the biomass of the tree, such as heart rot or insect damage; or any tree outside of the acceptable age range (≤ 15 years of the oldest tree in the stand).

Prior to harvest, DBH (diameter at breast height, 1.37m) was measured and crown width was estimated using a meter tape. After felling of the tree, total height and height to crown base were measured. Crown base was defined as the point along the bole at the bottom of roughly 90% of the crown mass, and crown length was calculated as:

$$CL = H - HCB \quad (1)$$

where CL = crown length, H = total tree height, and HCB = height to the base of the live crown.

Aboveground Components

Tree Bole - Each bole was harvested at ground level and all branches were removed. The bole was cut into three to four sections with 1 to 2 discs cut out as subsamples to determine moisture content for dry weight. For each bole, two discs were always taken at DBH, and at 90% of crown base (the location on the bole where most of the crown began). Two discs were taken from each section if the bole forked near the top or if DBH and crown base were one meter or closer in proximity. Each bole section was weighed separately using a digital hanging scale and the disc weight of the subsample was added back into the weight for its respective section. Discs were then dried to a constant weight at 70°C in the lab to determine moisture content. Dry: wet weight ratio for each disc was then applied to determine dry weight of the entire bole section. For each DBH and crown base subsample, the following measurements were taken for determining sapwood area: phloem + bark thickness, total diameter, and heartwood diameter. Two perpendicular measurements were taken and averaged for each of these parameters except for diameter at breast height, which was measured with a diameter tape prior to harvest. Sapwood diameter can be determined by subtracting the diameter of phloem + bark and heartwood diameter from total diameter. Therefore, the following equation was used to determine sapwood area:

$$SA = a - b \quad (2)$$

where SA = Sapwood Area, a = the basal area excluding phloem and bark, and b = heartwood area.

Branches - Branches were cut flush with the tree bole and were separated from foliage at 6.4 mm in diameter. Thus, branches consisted of all shoots minus the tree bole that were greater than 6.4 mm in diameter, because biomass smaller than 6.4 mm are likely to be consumed by fire (Despain 1990), allowing for post-fire estimates of branch biomass, independent of small twigs

that were likely to be consumed the fire. Branches were compiled rather than separated into three crown sections, because one subsample from all sections was deemed sufficient to determine the dry weight of the entire component. A subsample of approximately 4.0 L was taken to determine moisture content for dry weight for each tree, where it was then dried in the lab.

Fine Fuels - The fine fuels component was considered to be all needles and associated twigs less than 6.4 mm in diameter. These were combined because needles and twigs smaller than 6.4 mm diameter are likely to be consumed by fire (Despain 1990). The fine fuels component was maintained in separate piles of lower, middle, and upper crown sections for each tree, since foliage moisture contents were likely to vary with crown height (Brown 1978). A random subsample approximating the size of approximately 4.0 L volume was taken from each crown section to determine moisture content. The fine fuels subsamples were then weighed to obtain wet weight. If immediate weighing was not possible, subsamples were stored in a cooler for no more than 5 days in plastic bags, to prevent moisture loss prior to weighing.

The current year's growth (2004) was removed and discarded, because many of the needles were not fully expanded, and samples were collected at varying times throughout the summer of 2004. The subsample was weighed again to determine the proportion of the fine fuels component from the current year's growth. This proportion was then subtracted from the entire foliage component. After weighing, a random sample of 10 needle fascicles was taken from each fine fuels subsample, and the length and width of each fascicle was measured to determine leaf area. A tapered, bisected cylinder was used to determine surface area represented by each fascicle (Pearson et al. 1984 ; Madgwick 1964). This sample was dried and subsequently weighed so that surface area of this subsample could be extrapolated to the entire tree's needle

biomass. This sample was also weighed while still wet for subsequent drying and weighing to determine moisture content for dry weight determination of total needle biomass. The dry weight proportion of total foliage biomass that was needles was determined from separating needles from twigs after the foliage subsamples were dried.

Belowground Components

For each tree, the entire coarse root system (>10mm diameter) was excavated with the encouragement of a backhoe or come-a-long. Prior to excavation, smaller roots (\approx 10-20 cm) that could potentially be damaged by the backhoe or other excavation techniques were removed by hand. After excavation, the root system was divided into four size classes: root crown (i.e. the massive structure directly beneath the tree bole), lateral roots >50mm in diameter, lateral roots 25-50mm in diameter, and lateral roots 10-25mm in diameter. Total weight of each root size class was weighed using a digital hanging scale (Salter-Brecknell). Subsamples were taken and weighed to determine moisture content for dry weight of each size class. Subsamples were then dried at approximately 70°C where the dry: wet weight ratio was applied to its corresponding size class for determination of total coarse root system dry weight.

Stand Level Biomass Estimations

The allometric models derived from three stands varying in densities and ages were used to determine biomass allocation patterns for above and belowground components of lodgepole pine in the three study sites. From variable radius point sampling (Avery and Burkhardt 1994), tree diameters were measured at six points within each stand. Basal area could then be calculated. In order to estimate total height and height to the base of the live crown in each stand, regression equations between DBH and total height and between total height and crown base were used.

However, if the relationship from those regressions was not significant ($p > 0.05$), the mean of height or height to crown base for each of three diameter classes was applied to all trees in their respective diameter classes. These measured and estimated parameters were used in the application of allometric equations for various tree components from this study and were then applied to the trees measured in variable radius point sampling (Avery and Burkhart 1994).

There were two sources of error when estimating stand level biomass: (1) the error associated with using regression equations for biomass determination of the trees measured in variable point sampling; and (2) the plot level error associated with the variable radius point sampling method itself. However, the accumulated error from error (1) is actually included in error (2).

Therefore, the perceived problem of error accumulation does not actually exist (Giardina and Ryan 2002), and comparisons of stand biomass between densities and ages remain valid (see *below*).

Carbon Storage

Approximately 48% of the dry weight of a lodgepole pine is comprised of carbon (C) (Koch 1996). The carbon storage for our study was compared against other lodgepole pine studies and forested biomes.

Statistical Analyses

Model Development

All allometric models were developed with SPSS 13.0 (SPSS Inc. 2005). Models for each tree component (Table 2) were developed for the three individual stands, for all sites combined, and were also pooled by density and age. The following criteria were used to develop the best models for predicting biomass of lodgepole pine:

A.) The model must be biologically reasonable (Hilborn and Mangel 1997). For instance, an exponential model may yield the highest coefficient of determination (R^2) for predicting total coarse root biomass with tree basal area, but an exponential increase in root biomass with basal area is not biologically reasonable.

B.) The model must be of a form (linear or non-linear) that fits the data, although a model that does not produce a proper fit may achieve a higher R^2 . The proper model form was chosen using the following methods:

1. All potential predictors were plotted against each biomass component.
2. For any given plot, if a relationship was observed, data were examined to determine its linearity of curvilinearity.
3. To detect more subtle patterns of linearity or curvilinearity of data, the predictor was plotted against its residuals. If the relationship was linear ($y = ax + b$), a shotgun pattern around the horizontal axis through the origin was apparent. If the pattern appeared to be curvilinear, a curvilinear analysis was chosen. A nonlinear power function best fit much of our data.
4. Where more than one predictor exhibited a non-linear relationship, coefficients of determination (R^2), mean square errors, and plots of residuals were used to determine the best model. In addition, multiple predictors were combined into a multiplicative power model ($y = a x^b x_2^c$) and compared to models with one predictor.

C. If two predictors were deemed to be relatively equal based on their biological plausibility, coefficient of determination (r^2/R^2), standard error / mean square error, and plot of the residuals, the most easily measured independent variable was chosen.

Model Comparison

Density and Age

To determine whether allometric models differed between stands of varying densities and ages, the sum of squares of the residuals for each model, pooled by density and age, were compared using the extra sum of squares analysis for nested models (Bates and Watts 1988). In addition, equations for total aboveground biomass and coarse root biomass were used to predict biomass in a different stand from where they were developed. For instance, pooled equations from the two young stands were used to predict above and belowground biomass in the older stand, to determine the degree of error produced from using an inappropriate model.

Geographic Location Comparisons

Models for mature lodgepole pine forests in this study were compared to models developed by Pearson et al. (1984) in the Medicine Bow Mountains of southeastern Wyoming and by Comeau and Kimmins (1989) in British Columbia. These models were used to estimate biomass using the same measured parameters used to develop allometric models for this study. Selected models were similar in stand density and age to allometric models developed for this study. Comparison was further facilitated by selecting sites from this study that were similar to stands used to develop the models for Pearson et al. (1984) and Comeau and Kimmins (1989). Paired, two-tailed t-tests were used to assess whether biomass estimates from this study differed statistically from biomass estimates produced from other models (Comeau and Kimmins 1989); (Pearson et al. 1984) ($\alpha = 0.05$). In addition, actual biomass values from this study were compared against values estimated from the application of our allometric models to determine whether our estimated biomass values were more similar to the actual values than estimated

values calculated from the application of models developed by Pearson et al. (1984) and Comeau and Kimmins (1989).

Comparing Biomass Allocation Patterns

To determine whether allocation patterns at the stand and tree level differed between density and age, one-way ANOVAs were conducted, followed by Tukey's HSD post-hoc analyses. The following variables were used for comparisons: total coarse root biomass: total aboveground biomass; root crown: lateral root biomass; and percent of total biomass for bole, branches, and foliage. (*Note: The total coarse root biomass: total aboveground biomass ratio will be referred to in the following text as the below: aboveground biomass ratio.*)

RESULTS

ALLOMETRIC MODEL DEVELOPMENT

Model summary

Forty-eight allometric models for all measured tree components are shown in Table 2. R^2 values ranged from 0.54 to 0.99, and 37 out of 48 of the models had R^2 values greater than 0.80. Generally, for any given component, model strength decreased with increasing tree size, indicating greater variability in the biomass of larger trees than smaller trees. Volume (basal area (cm^2) * total height (cm)) was the best predictor of total aboveground and bole biomass across all stand densities and ages. Basal area (cm^2) was the best predictor of coarse root biomass, root crown biomass, and lateral root biomass. Best predictors of branch biomass were basal area and crown length, while basal area and sapwood area best predicted foliage and needle biomass (Table 2). Allometric models for total aboveground biomass, bole biomass, total coarse root biomass, and lateral root biomass were the most robust models, because only 1 of those 24 models had R^2 values below 0.89. In contrast, the other 24 models, which were for root crown,

branches, fine fuels, and needles were less robust, because R^2 values were below 0.80 for 9 of the 24 models. For total aboveground biomass, the best model was for all sites combined ($R^2 = 0.95$). Pooling the stands by age ($R^2(\text{old}) = 0.94$, $R^2(\text{young}) = 0.95$) produced better models than pooling stands by density ($R^2(\text{dense}) = 0.84$, $R^2(\text{sparse}) = 0.94$). The same pattern was observed for bole biomass, branch biomass, and root biomass components (Table 2). An exception for this is lateral root biomass where 94% of the variation in lateral root biomass was explained by basal area after developing separate models stratified by age, compared to stratification by stand density where 89% and 91% of the variation in lateral root biomass was explained by basal area for the two sparse stands and the single dense stand, respectively.

Model Comparisons Between Densities and Ages

Where statistical model comparisons were possible, most allometric models differed significantly between densities and ages ($p < 0.05$, Table 3.). Although formal statistical comparisons were not possible if either the model form or the predictor variables between two models were considered to be different, those models were nevertheless considered to be qualitatively different, because the allometric relationships were different. However, models for the tree bole (extra sum of squares, $p = 0.622$), root crown (extra sum of squares, $p = 0.396$), and lateral roots (extra sum of squares, $p = 0.608$) were not significantly different when stands were pooled by density, and models for root crowns (extra sum of squares, $p = 0.036$) and lateral roots (extra sum of squares, $p = 0.020$) were only modestly different. In addition, equations for total aboveground biomass were less different when pooled by density (extra sum of squares, $p = 0.037$) than by age (extra sum of squares, $p < 0.001$).

Model Comparison Between Geographic Locations

Generally, predicted biomass values from equations developed in this study were closer to actual biomass of lodgepole pine in the Greater Yellowstone Ecosystem than predicted values from equations developed by Comeau and Kimmins (1989) and Pearson et al. (1984) (paired t-test, $p < 0.05$, Table 4, Figure 2 and 3). Predicted values applying our study's equations typically produced biomass values that were not significantly different (paired t-test, $p > 0.05$) from actual biomass values. However, estimates of branch biomass applying Pearson et al.'s equations were slightly more similar to actual values (paired t-test, $p = 0.005$) than were estimated values applying our equations (paired t-test, $p = 0.003$). Although Pearson et al.'s models appeared to be better at predicting actual branch biomass in the GYE according to paired t-tests, more in-depth examination of Table 4 revealed a different pattern, because the mean value for branch biomass was closer to the actual value when applying this study's equations. In addition, Figure 3 identified a clear departure of Pearson et al.'s values from the actual values with increasing tree diameter, while this study's predicted values followed the actual values more closely with increasing diameter. An additional caveat is for the comparison between bole biomass for this study and bole biomass for Pearson et al.'s study, because Pearson et al.'s predicted values for bole biomass were statistically similar (paired t-test, $p = 0.063$) to actual bole biomass from this study. However, predicting bole biomass with our study's equations produced predicted bole biomass values that were more similar to actual bole biomass values from this study ($p = 0.514$). The greatest difference in observed versus predicted biomass between studies was for larger trees (Table 4, Figure 2 and 3), supporting the observation of increased variation in allometric models with increasing tree size. Biomass estimates produced by models from studies northwest (Comeau and Kimmins 1989) and southeast (Pearson et al. 1984) of the GYE produced significantly lower estimates of root biomass, higher estimates of needle and branch biomass,

and relatively comparable estimates of bole biomass (Table 4, Figure 2, 3). The root biomass estimates generated from models developed in the Medicine Bow Mountains produced slightly lower biomass estimates than from this study (Table 4, Figure 3). However, a portion of this difference is probably attributed to differences in the definition of a root crown between studies. For this study, a root crown was the portion of the coarse root system that is directly below the basal swell of the tree bole and within the lateral extent of the diameter of the tree at ground level. In contrast, Pearson et al. (1984) defined the root crown as the structure directly below the basal swell of the tree bole extending laterally to a distance of $1.5 \times \text{DBH}$.

BIOMASS ALLOCATION PATTERNS

Individual Tree Level Allocation Patterns

Allocation to bole biomass was highest for all three stands, but there was considerable variability for allocation to other components. The hierarchy of biomass allocation for tree level biomass allocation patterns was as follows: for the OS and YD stands it was bole > foliage > total coarse root biomass > branches, and for the YS stand it was bole > foliage > branches > total coarse root biomass (Table 5, Figure 4). Aboveground biomass was lowest for the YD and highest for the OS stand (Table 5). A striking result of the ANOVA for biomass allocation within trees was that the most structurally dissimilar stands (OS and YD) had the most similar biomass allocation patterns ($p > 0.05$, Table 5, Figure 4), except for the below: aboveground biomass ratio, where the OS and YD stands were significantly different from one another (Figure 4). In contrast, neither the OS and YS stands, nor the YS and YD stands were significantly different from one another (Table 6). Although differences were not significant according to the one-way ANOVA ($p > 0.05$) (Table 6), the root crown: lateral root ratio was lowest for the YS stand and highest for the YD stand (Table 5). The tree bole as a proportion of total tree biomass

was highest for the YD stand and lowest for the YS stand (Table 5, Figure 4) while in contrast, branches, foliage, and needles as a proportion of total tree biomass were highest in the YS stand.

Stand Level Allocation Patterns

The hierarchy of stand level biomass allocation for lodgepole pine in the GYE was similar to the pattern observed for the individual tree level, and was as follows: for both the OS stand and YD stands it was bole > foliage > total coarse root biomass > branches; and for the YS stand it was bole > foliage > branches > total coarse root biomass (Table 7, Figure 5). This indicated that bole biomass was the most dominant component of total tree biomass in all three stands. Similar to allocation patterns for individual trees, stand level biomass allocation was most similar for the most structurally dissimilar stands (OS and YD) (Table 7, Figure 5). The results of the one-way ANOVA revealed that stand density and age did not affect how stands allocated their biomass with respect to below: aboveground biomass ($p = 0.07$) (Table 6), although not statistically different, the two young stands did have slightly higher below: aboveground biomass ratios (0.12) than the OS stand (0.10) (Table 7). For the ratio of root crown: lateral root biomass, post-hoc analyses (Table 6) showed that the ratio of root crown: lateral root biomass was more affected by stand age than by stand density; there was no difference between the YS and YD stand ($p = 0.719$), but there was a significant difference when comparing the OS stand to both the YS ($p = 0.010$), and YD ($p = 0.001$) stands (Table 6). In addition, the root crown: lateral root ratio for each stand revealed a similar pattern, where it was 2.2 for the OS stand and 1.4 and 1.5 for the YS and YD stands respectively (Table 7), indicating a stronger effect of stand age than density on belowground allocation. The percentage of total biomass allocated to the tree bole was strongly affected by stand density and age, and all allocation comparisons between stands were significantly different ($p < 0.05$) (Figure 5).

Allocation to the tree bole differed for all three stands, and it was higher for the OS and YD stands than the YS stand (Table 7, Figure 5). In contrast, allocation to branches, foliage, and needles was highest in the YS stand, and lower in the OS and YD stands (Table 7, Figure 5). Leaf Area Index (LAI) was approximately twice as high in the sparse stands compared to the YD stand, but was quite similar between the OS and YS stands (Table 7).

Carbon Storage in the Greater Yellowstone Ecosystem compared to other forests

The patterns found for biomass allocation were identical for carbon storage (Table 8), because biomass of lodgepole pine is approximately 48% C (Koch 1996). Carbon storage for total aboveground tree biomass was 70.0 Mg ha⁻¹ for the OS stand, 40.8 Mg ha⁻¹ for the YS stand, and 46.7 Mg ha⁻¹ for the YD stand. For a 110-year-old lodgepole pine forest in another study from the GYE, total aboveground tree carbon storage was 86.9 Mg ha⁻¹ (Litton et al. 2004). For other forest types total aboveground tree biomass was 107.9 Mg ha⁻¹ for a 250-year-old *Pinus ponderosa* forest in central Oregon by (Law et al. 2001), 93.4 Mg ha⁻¹ for a 50-120-year-old temperate deciduous forest in eastern Tennessee (Curtis et al. 2002), 120.9-153.6 Mg ha⁻¹ for tropical forests of the southwestern Brazilian Amazon (Cummings et al. 2002), and 49.9 Mg ha⁻¹ and 39.3 Mg ha⁻¹ for 139-year-old and 66-year-old *Pinus sylvestris* forests respectively in boreal Euro-Siberia (Schulze et al. 1999).

Comparing biomass allocation patterns across geographic locations independent of stand density and age

When comparing stands from this study to stands in other studies that had similar densities and ages, the proportion of total biomass allocated to the tree bole was greater in this study when compared to Pearson et al.'s (1984) older stand, but was smaller for the younger stands when compared to both Pearson et al. and Comeau and Kimmins (Table 9, Figure 6). The

opposite pattern was shown for branches, although there are slight differences in the definition of branches among studies, because we excluded twigs < ¼” from our branches component (see *Methods*) (Table 9, Figure 6). The percentage of total biomass allocated to branches and needles was greater for our study than studies developed in southeastern WY and British Columbia for all stands except the OS stand (Table 9, Figure 6).

DISCUSSION

ALLOMETRIC MODEL DEVELOPMENT

Variation in stand density and age affected which of several measured tree morphometric parameters would best predict biomass of lodgepole pine tree components. The product of tree basal area and total height (volume) was the best predictor of total aboveground and bole biomass (Table 2). Notably, a tree’s ability to produce stemwood biomass, a major component of tree bole and total aboveground biomass, is strongly influenced by site productivity (Barnes et al. 1980). Therefore, a model including tree height, a variable relating more strongly to site productivity than any other measured parameter (Barnes et al. 1980), can explain a large amount of the variability in bole and total aboveground biomass. In contrast, tree height was not found to be a useful variable for predicting the biomass of other tree components (Table 2). In addition, the decrease in variability of the dependent variable that can be explained by its respective predictor with increasing tree size may be due to greater variability in biomass allocation patterns with increasing tree size.

Total coarse root biomass (>10 mm), root crown biomass, and lateral root biomass are best explained by tree basal area (Table 2), where tree diameter and basal area are measured parameters most closely correlating with spacing effects related to tree density (Barnes et al. 1980), suggesting coarse root biomass is at least partly dependent on tree spacing. Further

studies incorporating nearest neighbor methods may be needed to determine effects of spacing on the coarse root biomass of individual trees, such as the approach by (Mainwaring and Maguire 2004) where they modeled the relationship between spacing among individual trees and tree diameter growth for lodgepole and ponderosa pine in central Oregon. They found that spatially explicit models including distance-dependent measures of competition among trees explained more of the variability in tree diameter growth than did implicit measures of competition based on stand-level averages. Their results suggested that allometric models have the potential to be improved further by including explicit measures of competition.

Most of the variability in needle and foliage biomass is explained by basal area and sapwood area (Table 2). Sapwood area has been found to be a good predictor of foliage biomass in other studies (Snell 1978; Grier and Waring 1974; Pearson et al. 1984; Comeau and Kimmins 1989), because it is a good measure of a tree's ability to conduct water and nutrients (Taiz and Zeiger 2002). Needle and foliage biomass in the older stand was best explained either by sapwood area or a combination of sapwood and basal area (Table 2). This indicates foliage biomass may be better explained by a tree's ability to conduct water and nutrients in older forests where water and nutrients are more limiting (Smith and Long 2001; Berger et al. 2004; Ryan et al. 2004). In contrast, basal area was the single best predictor of foliage biomass in younger stands (Table 2), indicating that foliage biomass in younger forests is better explained by tree spacing rather than by the tree's ability to conduct water and nutrients.

Differences between densities and ages

Allometric models were expected to differ between densities and ages due to differences in biomass allocation patterns. For the most part, this was supported by the data (Table 3). However, models for tree bole, root crown, and lateral roots did not differ when pooled by

density, and models for aboveground biomass were less different when pooled by density than by age. One plausible explanation for this pattern is that stand densities may not have been different enough for some of the models to differ according to stand density or to be less different than for models pooled by age. Although 2,452 trees ha⁻¹ was considered in this study to be a dense stand, “dog-hair” stands of lodgepole pine that are of comparable age can sometimes reach densities higher than 10,000 trees ha⁻¹ (Koch 1996). Therefore, the relatively small difference in stand densities in this study may contribute to the relative similarity of models pooled by density compared with models pooled by age. Although allometric equations appear to be more similar across densities, application of models significantly different in density from where they were developed should be approached with caution. Furthermore, inappropriate model use can cause significant errors when extrapolating allometric equations to the landscape scale.

The estimated errors produced by inappropriate model use appeared to be related to differences in aboveground: belowground biomass allocation, where an overestimation of aboveground biomass was coupled with an underestimation of belowground biomass. Predicting biomass in the OS stand using the pooled model from the younger stands (YS and YD) produced tremendous error, where total aboveground biomass was 127.0 Mg/ha with the proper model for that stand, while it was nearly double (215.4 Mg ha⁻¹) using the improper model. For total coarse root biomass, the error was less pronounced, but still evident, where it was 12.1 Mg ha⁻¹ for the appropriate model and 10.2 Mg ha⁻¹ for the inappropriate model. Predicting biomass in the sparse stand using the model developed in the dense stand underestimated total aboveground biomass significantly, where it was 85.0 Mg ha⁻¹ for the correct model, but was 61.5 Mg ha⁻¹ for

the incorrect model. The inappropriate model overestimated for total coarse root biomass, it was 10.5 Mg ha⁻¹ for the appropriate model and 13.6 Mg ha⁻¹ for the inappropriate model.

Differences between Geographic Locations

Differences in allometric equations among geographic locations are likely attributed to differences in soil, topography, and climate. The soils on which Pearson et al. (1984) developed allometrics in the Medicine Bow Mountains were generally less infertile and were derived primarily from glacial till and fluvial conglomerates, while soils in British Columbia were Orthic Eutric Brunisols for xeric sites and Brunisolic Gray Luvisols for mesic sites (Comeau and Kimmins 1989). In contrast, soils of this study were more infertile and were developed on volcanic substrates (Bowerman et al. 1999). Sites where allometrics were developed by Comeau and Kimmins (1989) were more productive than sites in this study, where higher site index (SI), which is associated with higher productivity, ranged from 14.3 to 20.5m at 100 years for Comeau and Kimmins (1989) compared to our study where SI ranged from 14.3 to 16.0 at 100 years.

Bole biomass was the only component that did not differ between the GYE and the Medicine Bow Mountains (Pearson et al. 1984), and was the component most similar between the GYE and British Columbia (Comeau and Kimmins 1989), indicating that relationships between bole biomass and its predictor(s) (basal area and total height) are relatively constant across gradients of elevation, topography, climate, and site productivity. This further indicates that a tree will allocate a relatively constant proportion of available resources throughout its lifespan to wood production, indicating a tree may compensate for reductions in root and foliar biomass through increases in light, nutrient, and overall photosynthetic efficiency. However, increases in light use efficiency typically coincide with increases in leaf area (Smethurst et al.

2003). Therefore, the ability of a tree to produce wood across sites may be controlled by interactions between nutrient and light use efficiency, where a reduction in light use efficiency is coupled with an increase in nutrient use efficiency (Binkley et al. 2004). This finding is consistent with Tilman's (1982) resource ratio model of plant competition that implies stability among competing plants at different ratios of important resources, such as nitrogen and light (Gurevitch et al. 2002). Despite the relatively constant relationships between bole biomass and its predictors across geographic locations, predicted bole biomass values when applying our equations as opposed to those developed by Pearson et al. (1984) were closer to actual bole biomass (Table 4, Figure 3), indicating the need for using locally developed allometric models.

Needle biomass estimates were lower for less nutrient poor sites (Pearson et al. 1984; Comeau and Kimmins 1989) than for actual and predicted biomass from sites in the GYE (Table 4, Figure 3), indicating higher foliage biomass was increasing photosynthate to compensate for more nutrient limiting conditions that might otherwise decrease wood production. This potential balance between light use and nutrient availability may account for some of the homogeneity in bole biomass across geographic locations.

Root biomass in the GYE was over predicted by models developed in British Columbia and southeastern Wyoming, indicating root crown and coarse root biomass is dependent upon a site's ability to support production of wood biomass. This suggests that coarse root biomass has little impact on the trees ability to uptake water and nutrients, because less coarse root biomass should have been needed to uptake water and nutrients in British Columbia and southeastern Wyoming, which are more productive sites than the GYE.

The greatest difference in biomass of tree components across geographic locations was for larger trees (Figure 2, 3), indicating site conditions become increasingly important as forests

become older and trees become taller. This is attributed to an increase in nutrient limitation (Berger et al. 2004; Ryan et al. 1997; Smith and Resh 1999; Smith and Long 2001), hydraulic limitation (Ryan and Yoder 1997), and maintenance respiration (Ryan et al. 1995) with increases in stand age and tree height.

BIOMASS ALLOCATION PATTERNS

The results indicated (1) biomass allocation patterns differed between stand densities and ages; (2) biomass allocation patterns were different at the individual tree level than for the stand level; (3) however, allocation to coarse roots was relatively constant across stand densities and ages; (4) biomass allocation patterns were different in the GYE compared to southeastern Wyoming and British Columbia; and (5) carbon storage of mature lodgepole in the GYE was comparable to, but at the lower end of carbon storage published in other forest types and biomes.

Aboveground Biomass

Within the aboveground portion of individual lodgepole pine and lodgepole pine stands, biomass of branches, needles, and foliage were highest in the YS stand (Table 5,7, Figure 4,5). At the stand level, branches, needles, and foliage as a proportion of total tree biomass was lowest in the OS stand, indicating that there was ample room for development of a large tree crown in the YS stand, in contrast to the YD and OS stands where there was more competition. The OS stand had more crown competition than the YD stand, because tree spacing was more homogeneous in the OS stand; in contrast, the YS stand had heterogeneous tree spacing resulting in an assemblage of open grown and clumped trees (Table 1). In addition, the OS stand may have had the lowest branch, foliage, and needle biomass due to greater self-pruning of the lower branches in the older stand, a common characteristic of lodgepole pine (Koch 1996). Although not statistically significant, the YD stand had the lowest branch, needle, and foliage allocation,

indicating that greater self-pruning may occur with increasing stand density, and also indicating that the impact of self-pruning on biomass allocation is controlled by density in addition to age. Similarly, Pearson et al. (1984) found that a sparser stand (2217 trees/ha) had a greater amount of total biomass allocated to branches (8.3%) than for a denser stand on the same site (14,640 trees/ha), where only 5.2% of total tree biomass was allocated to branches.

Ryan et al. (1997) suggested that young trees allocate more resources to foliage rather than to woody components, and this trend becomes less pronounced with crown closure. This is supported by the results of this study, as the open-grown YS stand had 26.5% of total biomass allocated to foliage, while the OS stand with greater observed crown competition had 10.2% of total biomass allocated to foliage (Table 5, Figure 4). Pearson et al. (1984) found that allocation to foliage was greater in a young, sparse stand (75 years old), where allocation to foliage was 10.0% of total tree biomass, than in an older stand (110 years old), where foliage was only 6.2% of total tree biomass.

Allocation to tree boles was lowest in the YS stand at the individual tree and stand levels, while bole allocation to the OS and YD stands were surprisingly comparable to each other. The low proportion of total tree biomass for boles in the YS stand is likely attributed to a high proportion of branch and foliage biomass created by a combination of its young age and open-grown stand structure. The similarity in allocation to tree boles between the OS and YD stands may be related to their competitive similarity. Although not quantified, our observations suggested both of these stands possessed extensive crown competition, while the YS stand had less crown competition. Increased allocation to boles in dense and older stands with greater crown competition was consistent with the results of Nilsson and Albrekston (1993) and Kaufmann and Ryan (1986). They found that allocation to the tree bole compared to foliage was

greater for competitively suppressed trees. Future studies should include more direct measurements of competition among trees, such as nearest neighbor analyses.

Leaf Area Index

LAI was much greater in the sparse stands than in the YD stand, suggesting that tree canopies were much more suppressed in that stand, which is contrary to the results of Pearson et al. (1984). They found that a dense stand with 14,640 trees/ha had only a slightly lower LAI (7.1 m²/ha) than a less dense stand with 2,217 trees/ha (7.3 m²/ha). Overall, my estimates of LAI were much lower than estimates reported by Pearson et al. (1984), which could be attributed to lower stand basal areas for this study (Table 1). Basal areas for this study ranged from 16.84 – 28.32 m²/ha, but Pearson et al. (1984) reported basal areas from 26 – 64 m²/ha. Although sapwood area has been shown to be a better predictor of foliage mass and leaf area than basal area by Pearson et al. (1984) and by Grier and Waring (1974), basal area has also been shown to predict foliage mass and leaf area well (Pearson et al. 1984). Therefore, leaf area index should also be affected by basal area.

Belowground Biomass

For allocation to belowground biomass components at the stand level, the root crown: lateral root biomass ratio was found to be significantly less for younger stands than for the single old stand, indicating that the root crown becomes a more dominant part of root systems as stand age increases, suggesting a greater need for structural support as trees become older and larger. Similarly, the root crown: lateral root biomass ratio for individual trees revealed that allocation to root crowns was lowest for the YS stand, but similarly higher for the two stands differing most in density and age (OS and YD). The YS stand was the most open-grown of the three stands and likely had the least amount of competition among trees, indicating that the root crown becomes a

greater portion of the root system as belowground competition decreases. Interestingly, greater differences in stand age for the root crown: lateral root biomass ratio were evident when comparing sites at the stand level, while greater differences in stand density were revealed when examining the data at the individual tree level, indicating the importance of sampling at multiple scales for understanding biomass allocation patterns of lodgepole pine. A possible explanation for variability in allocation at differing scales is that individual tree allocation patterns are likely a function of individual tree age and tree spacing around individual trees, while in contrast, stand level allocation patterns are likely a function of the stand age and density.

Below: Aboveground Biomass Ratio

At the stand level, stand density and age had surprisingly little effect on the shifting of resources to above and belowground biomass, in contrast to a study by Pearson et al. (1984) for lodgepole pine in southeastern Wyoming. Differences in below: aboveground biomass partitioning among densities ranging from 420 to 14640 trees ha⁻¹ found by Pearson et al. may be at least partly attributed to the inclusion of roots smaller than 10mm diameter in their study. For this study, below: aboveground biomass was found to be constant across stand ages, which is comparable to estimates of total root biomass including fine roots across stand ages for other studies (Litton et al. 2004; Pearson et al. 1984). Despite the constant relative biomass partitioning of resources above and belowground at the stand level, below: aboveground biomass was considerably more variable at the scale of individual trees (Table 5, 7), because below: aboveground allocation was lowest in the YD stand, the site that likely had the highest belowground allocation, indicating that both stand density and age had an important effect on allocation to coarse root biomass. Although there are some similarities in the ratio of below:

aboveground biomass among sites, especially at the stand level, biomass partitioning within above and belowground components was found to be highly variable with stand density and age.

Carbon Storage in the Greater Yellowstone Ecosystem compared to other forests

Carbon storage for our study was comparable to another study in the GYE, and it was also comparable to carbon storage for other forest types and biomes. However, carbon storage in mature lodgepole pine trees was at the lower end of values reported for other forest types and biomes, and the results suggest that only boreal forests have lower carbon stored in aboveground tree biomass than subalpine lodgepole pine forests (Schulze et al. 1999).

Biomass Allocation Comparisons Among Geographic Locations

Although fine roots (<10mm diameter) were not considered in this study, direct comparisons for aboveground biomass components in different geographic regions could be made. The proportion of aboveground biomass allocated to the tree bole was significantly less for this study except for the comparison between older stands, and total bole biomass was less in this study for all stands (Figure 6). This suggests that allocation to the tree bole is in a large part driven by site productivity, because lodgepole pine forests in the GYE are less productive than lodgepole pine forests in southeastern Wyoming and in British Columbia due to a combination of poorer soils developed on volcanic rhyolite, more extreme climatic conditions, and differences in topography. In addition, site indices for this study ranged from 14.3 – 16.0m at 100 years, and site indices for Comeau and Kimmins (1989) ranged from 14.3 – 20.5 m at 100 years.

Furthermore, estimates of total root biomass were much lower for this study, although fine root biomass was excluded from this study (Figure 6), suggesting that total coarse root biomass is not driven by site productivity. Bole biomass allocation was found to be more constant across geographic locations for comparisons between older stands (Figure 6a), suggesting that during its

lifespan, lodgepole pine may gradually compensate for lower site productivities through increases in resource use efficiency in order to attain relatively constant wood production despite differences in site productivity (Binkley et al. 2004; Aber and Melillo 2001; Vitousek 1982). Interestingly, allocation to branches and needles was higher in the GYE than in British Columbia and southeastern Wyoming, suggesting that lodgepole pine in the GYE are compensating for poor site conditions by allocating more biomass to photosynthetic tissues and to branches for support of photosynthetic tissues, although nitrogen and other soil nutrients would be needed to produce these tissues. Therefore, lodgepole pine in the GYE may have greater nutrient use efficiency than lodgepole pine in British Columbia and southeastern Wyoming, although there are no data to support this, and future research is needed on the variability of nutrient use efficiency of lodgepole pine across a gradient of site productivities in the intermountain west.

SUMMARY AND CONCLUSIONS

ALLOMETRIC MODEL DEVELOPMENT

Allometric models developed for mature lodgepole pine in the Greater Yellowstone Ecosystem were very robust for predicting tree biomass and showed promise for estimating landscape level biomass of lodgepole pine forests, because R^2 values were often above 0.80. Allometric equations were found to differ between stand densities and ages according to statistical tests and qualitative observations, and they were also identified to be different among geographic locations independent of stand density and age. In addition, applications of inappropriate models sometimes produced tremendous errors and have the potential to do so in further applications. Therefore, wise use of these models is critical, as application of the appropriate model to the appropriate stand is vital due to differences identified by this study among forest structures and geographic locations. We strongly suggest that models not be

applied to stands differing significantly in density and age from the stands where the models were developed, and that models not be applied to geographic locations of considerable distance from where the models were developed. In addition, allometric models developed in this study have many potential uses from determination of NPP for carbon studies using multi-year measurements, fire modeling, and for determination of wood biomass by foresters.

BIOMASS ALLOCATION PATTERNS

The allocation of resources to above and belowground lodgepole pine biomass was relatively similar between stand densities and ages as shown by the relatively constant ratios of total coarse root: total aboveground biomass. Therefore, allocation to coarse root biomass is relatively constant across forest structures. However, there was considerable variability in aboveground allocation and belowground allocation when considered independently, because the ratio of root crown: lateral root biomass differed significantly with stand density and age, and allocation to the tree bole, branches, fine fuels, and needles differed with stand density and age. In addition above and belowground allocation patterns were affected differently and the individual tree and stand levels.

There were considerable differences in the biomass allocation patterns of lodgepole pine among geographic locations. Despite some similarities, generalizing patterns of biomass allocation across forest structures and among geographic locations should proceed with caution, and further research into the biomass allocation patterns of lodgepole pine in the Greater Yellowstone Ecosystem and elsewhere in the Intermountain West is needed. However, if further research indicates that the ratio of coarse root: total aboveground biomass for lodgepole pine stands is approximately 0.10 to 0.12 as identified by this study, determination of belowground lodgepole pine biomass could become considerably easier, because only aboveground

measurements would be needed and the appropriate ratio could be applied to determine coarse root biomass.

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Table 1. Sites for the development of allometric equations in the Greater Yellowstone Ecosystem.

Site Name	Elevation (m)	NAD 83, UTM Zone 12		Stand Age (years)	Stand Density (trees > 5cm DBH per hectare)	Stand basal area (m ² per hectare)
		Northing (m)	Easting (m)			
Grassy Lake	2249	4886015	511735	165	674	16.84
Coffee Pot	1951	4926541	472232	64	725	19.71
US 20	1951	4925932	472657	64	2452	28.32

Table 2. Allometric equations for predicting biomass (Kg) of eight different above and belowground components of *P. contorta* in the Greater Yellowstone Ecosystem.

Non Linear Power Functions ($y = ax^b$, or $y = ax^b x_2^c$)									
(Y)	(X)	Site(s)	DBH range (cm)	n	a	b	c	R ²	MSE
Total Aboveground Biomass	Volume**	All Sites	5.4 - 33.3	46	0.005	0.793	-	0.95	679.6
	-	Old, Sparse	11.3 - 33.3	17	0.003	0.817	-	0.94	758.4
	-	Young, Dense	5.4 - 15.6	14	0.00004	1.155	-	0.84	109.9
	-	Young, Sparse	11.7 - 25.0	15	0.0004	1.001	-	0.92	445.2
	-	2 Young Stands	5.4 - 25.0	29	0.0001	1.088	-	0.95	289.4
	-	2 Sparse Stands	11.3 - 33.3	32	0.010	0.741	-	0.94	810.0
Total Coarse Root Biomass (>10mm)	Basal Area (cm ²)	All Sites	5.4 - 32.0	24	0.028	1.139	-	0.95	11.8
	-	Old, Sparse	11.3 - 32.0	5	0.188	0.845	-	0.93	36.4
	-	Young, Dense	5.4 - 15.6	14	0.005	1.467	-	0.98	0.3
	-	Young, Sparse	12.7 - 24.3	5	0.002	1.579	-	0.95	8.3
	-	2 Young Stands	5.4 - 24.3	19	0.006	1.406	-	0.97	2.0
	-	2 Sparse Stands	11.3 - 32.0	10	29.939	-0.179	-	0.99	5.8
Root Crown Biomass	Basal Area (cm ²)	All Sites	5.4 - 32.0	24	0.020	1.109	-	0.84	13.6
	-	Old, Sparse	11.3 - 32.0	5	0.224	0.745	-	0.71	65.5
	-	Young, Dense	5.4 - 15.6	14	0.007	1.267	-	0.93	0.2
	-	Young, Sparse	12.7 - 24.3	5	0.007	1.284	-	0.89	5.3
	-	2 Young Stands	5.4 - 24.3	19	0.006	1.304	-	0.95	1.1
	-	2 Sparse Stands	11.3 - 32.0	10	0.050	0.968	-	0.73	33.8
Lateral Root Biomass (>10mm)	Basal Area (cm ²)	All Sites	5.4 - 32.0	24	0.008	1.193	-	0.94	2.1
	-	Old, Sparse	11.3 - 32.0	5	0.010	1.146	-	0.94	4.8
	-	Young, Dense	5.4 - 15.6	14	0.0004	1.738	-	0.91	0.2
	-	Young, Sparse	12.7 - 24.3	5	0.00003	2.153	-	0.94	2.6
	-	2 Young Stands	5.4 - 24.3	19	0.001	1.564	-	0.94	1.0
	-	2 Sparse Stands	11.3 - 32.0	10	0.011	1.147	-	0.89	5.2
Branches	Basal Area (cm ²), Crown Length ₂ (m)	All Sites	5.4 - 33.3	46	0.022	0.683	1.276	0.69	69.3
	-	Old, Sparse	11.3 - 33.3	17	0.003	1.136	0.850	0.86	21.6
	Basal Area (cm ²)	Young, Dense	5.4 - 15.6	14	0.002	1.548	-	0.91	0.4
	-	Young, Sparse	11.7 - 25.0	15	0.004	1.497	-	0.76	67.9
	Basal Area (cm ²), Crown Length ₂ (m)	2 Young Stands	5.4 - 25.0	29	0.001	1.855	-0.291	0.88	34.6
	-	2 Sparse Stands	11.3 - 33.3	32	0.042	0.528	1.288	0.54	96.2
Fine Fuels	Basal Area (cm ²), Sapwood Area ₂ (cm ²)	All Sites	5.4 - 33.3	46	0.418	0.466	0.418	0.68	184.8
	-	Old, Sparse	11.3 - 33.3	17	0.524	0.323	0.403	0.81	58.3

	Basal Area (cm ²)	Young, Dense	5.4 - 15.6	14	0.002	1.695	-	0.96	1.4
	-	Young, Sparse	11.7 - 25.0	15	0.011	1.427	-	0.86	97.1
	-	2 Young Stands	5.4 - 25.0	29	0.007	1.512	-	0.93	48.7
	Sapwood Area (cm ²)	2 Sparse Stands	11.3 - 33.3	32	1.204	0.638	-	0.52	220.9
Needles	Basal Area (cm ²), Sapwood Area ₂ (cm ²)	All Sites	5.4 - 33.3	46	0.192	0.525	0.317	0.73	67.0
	-	Old, Sparse	11.3 - 33.3	17	0.249	0.323	0.471	0.82	33.0
	Basal Area (cm ²)	Young, Dense	5.4 - 15.6	14	0.002	1.600	-	0.91	1.5
	-	Young, Sparse	11.7 - 25.0	15	0.014	1.312	-	0.78	60.3
	-	2 Young Stands	5.4 - 25.0	29	0.007	1.426	-	0.89	30.7
	Sapwood Area (cm ²)	2 Sparse Stands	11.3 - 33.3	32	0.563	0.701	-	0.61	78.5
Tree Bole	Volume**	Old, Sparse	11.3 - 33.3	17	0.002	0.822	-	0.93	608.5

(Linear Models, $y = ax + b$)

(Y)	(X)	Site(s)	DBH range (cm)	<i>n</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²	SE
Tree Bole	Volume**	All Sites	5.4 - 33.3	46	0.0002	3.420	-	0.96	17.9
	-	Young, Dense	5.4 - 15.6	14	0.0002	-0.327	-	0.79	8.9
	-	Young, Sparse	11.7 - 25.0	15	0.0002	0.055	-	0.95	7.6
	-	2 Young Stands	5.4 - 25.0	29	0.0002	5.482	-	0.93	8.9
	-	2 Sparse Stands	11.3 - 33.3	32	0.0002	1.921	-	0.95	20.8

Note: Non-linear power functions are listed first, and linear equations are at the end of the table. MSE is the mean square error for non-linear models, SE is the standard error of the estimate for linear models, *n* is the sample size, and *a*, *b*, and *c* are constants. X is the morphometric predictor variable and Y represents the response variable (biomass (Kg)). The subscript ₂ is for predictors that are associated with the coefficient *c* in non-linear models. ** Volume is the product of basal area in cm² and height in meters.

Table 3. Allometric equation comparison between densities and ages of mature *P. contorta* stands in the Greater Yellowstone Ecosystem derived from the extra sum of squares analysis for nested models (Bates and Watts 1988).

Dependent Variable	Model Comparison	F	p-value
Total Aboveground Biomass	Old vs. Young	11.726	<.0001*
Total Aboveground Biomass	Sparse vs. Dense	3.514	0.037*
Branches	Old vs. Young	19.706	<.0001*
Total Coarse Roots (>10mm)	Old vs. Young	8.128	<.0001*
Total Coarse Roots (>10mm)	Sparse vs. Dense	57.919	<.0001*
Root Crown	Old vs. Young	3.937	0.036*
Lateral Root Biomass (>10mm)	Old vs. Young	4.790	0.020*
Bole	Sparse vs. Dense	0.481	0.622
Root Crown	Sparse vs. Dense	0.971	0.396
Lateral Root Biomass	Sparse vs. Dense	0.508	0.608

Note: The * denotes significant differences ($\alpha = 0.05$). All possible statistical comparisons are shown. Equations for comparisons not in this table had different model forms.

Table 4. Comparison of actual *P. contorta* individual tree biomass vs. estimates from this study in the Greater Yellowstone Ecosystem and from studies in British Columbia by Comeau and Kimmins (1989) and Pearson et al. (1984).

Component	Site	Minimum Biomass (Kg)	Maximum Biomass (Kg)	Mean Biomass (Kg)	Age Range	Density Range	p-value
Bole	This Study (Actual)	10.2	136.8	50.7	64	725 - 2452	
	This Study (Predicted)	3.3	135.5	51.1	-	-	0.804
	Comeau and Kimmins	6.7	170.9	67.9	70 - 78	1770 - 3580	*<0.001
Branches	This Study (Actual)	0.3	55.9	14.0	64	725 - 2452	
	This Study (Predicted)	0.3	47.6	14.9	-	-	0.401
	Comeau and Kimmins	0.7	33.2	9.6	70 - 78	1770 - 3580	*0.037
Needles	This Study (Actual)	0.2	59.3	16.2	64	725 - 2452	
	This Study (Predicted)	0.6	48.1	16.5	-	-	0.739
	Comeau and Kimmins	0.4	24.5	5.5	70 - 78	1770 - 3580	*<0.001
Total Root	This Study (Actual)	0.7	33.8	8.1	64	725 - 2452	
	This Study (Predicted)	0.4	32.5	8.3	-	-	0.400
	Comeau and Kimmins	5.8	32.1	15.0	70 - 78	1770 - 3580	*<0.001
Bole	This Study (Actual)	26.0	329.0	137.1	64 - 165	674 - 2452	
	This Study (Predicted)	7.0	339.8	106.3	-	-	0.514
	Pearson et al.	24.7	256.6	121.8	75 - 240	<2500	*0.063
Branches	This Study (Actual)	1.7	55.9	21.7	64 - 165	674 - 725	
	This Study (Predicted)	3.1	29.1	16.0	-	-	*0.003
	Pearson et al.	3.2	32.9	15.6	75 - 240	<2500	*0.005
Needles	This Study (Actual)	1.6	44.7	25.8	165	674	
	This Study (Predicted)	8.5	45.4	25.9	-	-	0.928
	Pearson et al.	9.3	30.3	17.1	240	420	*<0.001
Root Crown	This Study (Actual)	0.6	35.9	7.7	74-165	674 - 2452	
	This Study (Predicted)	0.5	33.4	7.9	-	-	0.763
	Pearson et al.	-0.1	54.1	13.2	75 - 240	<2500	*<0.001

Note: The * denotes significant differences ($\alpha = 0.05$). The upper p-value for each component is the comparison between actual values from this study and predicted values from this study, and the lower p-value is for the comparison between actual values from this study and predicted values applying the equations from other studies.

Table 5. Biomass, carbon content, percent of total biomass and carbon, total coarse root: total aboveground biomass ratio, and root crown: lateral root biomass ratio at the individual tree and stand levels for three *Pinus contorta* stands in the GYE.

Component Biomass	- TREE LEVEL -								
	Old, Sparse			Young, Sparse			Young, Dense		
	Biomass (Mg/ha)	Carbon (Mg/ha)	%	Biomass Mg/ha	Carbon Mg/ha	%	Biomass Mg/ha	Carbon Mg/ha	%
Total Aboveground Biomass	187.9		86.3	128.9		87.6	41.0		90.1
Bole	141.2		64.8	59.7		40.6	31.2		68.7
Branches	14.9		6.9	24.3		16.5	2.7		5.9
Fine Fuels	31.8		14.6	44.9		30.6	7.1		15.6
Needles	25.8		11.8	27.0		18.4	4.6		10.1
Total Roots (>10mm)	30.0		13.7	18.2		12.4	4.5		9.9
Root Crown	19.0		8.7	10.4		7.1	2.6		5.7
Lateral Roots (>10mm)	11.0		5.0	7.8		5.3	1.9		4.2
Total Tree Biomass	217.9		100.0	147.1		100.0	45.5		100.1
Total Coarse Root: Total Aboveground Biomass		0.16 a			0.14 a			0.11 b	
Root Crown: Lateral Root Biomass		1.8 a			1.4 a			2.2 a	
Component Biomass	- STAND LEVEL -								
	Old, Sparse			Young, Sparse			Young, Dense		
	Biomass (Mg/ha)	Carbon (Mg/ha)	%	Biomass Mg/ha	Carbon Mg/ha	%	Biomass Mg/ha	Carbon Mg/ha	%
Total Aboveground Biomass	127.0	70.0	91.3	84.9	40.8	89.0	97.3	46.7	89.5
Bole	91.6	44.0	75.1	42.2	20.3	47.3	70.7	33.9	64.3
Branches	5.9	2.8	4.8	12.9	6.2	14.4	8.7	4.2	7.9
Fine Fuels	12.4	6.0	10.2	23.7	11.4	26.5	19.0	9.1	17.3
Needles	8.3	4.0	6.8	15.4	7.4	17.2	11.5	5.5	10.5
Total Root Biomass (>10mm)	12.1	5.8	8.7	10.5	5.0	11.0	11.5	5.5	10.5
Root Crown	8.2	4.0	6.7	6.6	3.2	7.4	7.1	3.4	6.5
Lateral Roots	3.7	1.8	3.0	4.5	2.2	5.0	4.8	2.3	4.4
Total Tree Biomass	139.1	66.8	100.0	95.4	45.8	100.0	108.8	52.2	100.0
Total Coarse Root: Total Aboveground Biomass		0.10 a			0.12 a			0.12 a	
Root Crown: Lateral Root Biomass		2.2 a			1.4 b			1.5 b	

Note: All components except for total tree biomass were derived from individual allometric models developed in this study; therefore, small discrepancies exist between total aboveground biomass and its components, as well as between total root biomass and its components. Different letters for ratios denote significance.

Table 6: Comparison of biomass and percent of total biomass for three *Pinus contorta* stands in the GYE to stands in British Columbia by Comeau and Kimmins (1989) and in southeast Wyoming by Pearson et al. (1989).

Comparisons			Total Aboveground		Tree Bole		Branches		Needles	
Study	Age	Density	Biomass (Mg/ha)	%	Biomass (Mg/ha)	%	Biomass (Mg/ha)	%	Biomass (Mg/ha)	%
This Study	64	2452	97.3	89.5	70.7	64.3	8.7	8.0	11.5	8.4
Comeau and Kimmins	70	1900	119.4	76.5	107.4	68.8	7.1	4.6	4.9	3.1
This Study	165	674	127.0	91.3	91.6	75.1	5.9	4.8	8.3	5.4
Pearson et al.	240	420	131.9	77.5	110.8	65.1	14.2	8.3	6.9	4.1
This Study	64	725	84.9	89.0	42.2	47.3	12.9	14.5	15.4	11.3
Pearson et al.	75	1280	96.3	78.4	74.4	60.6	9.6	7.8	12.3	10.0

Figure 1. Three Stands Differing in Densities and Ages for allometric model development of *P. contorta* in the Greater Yellowstone Ecosystem. Individual stands are depicted by a black square.

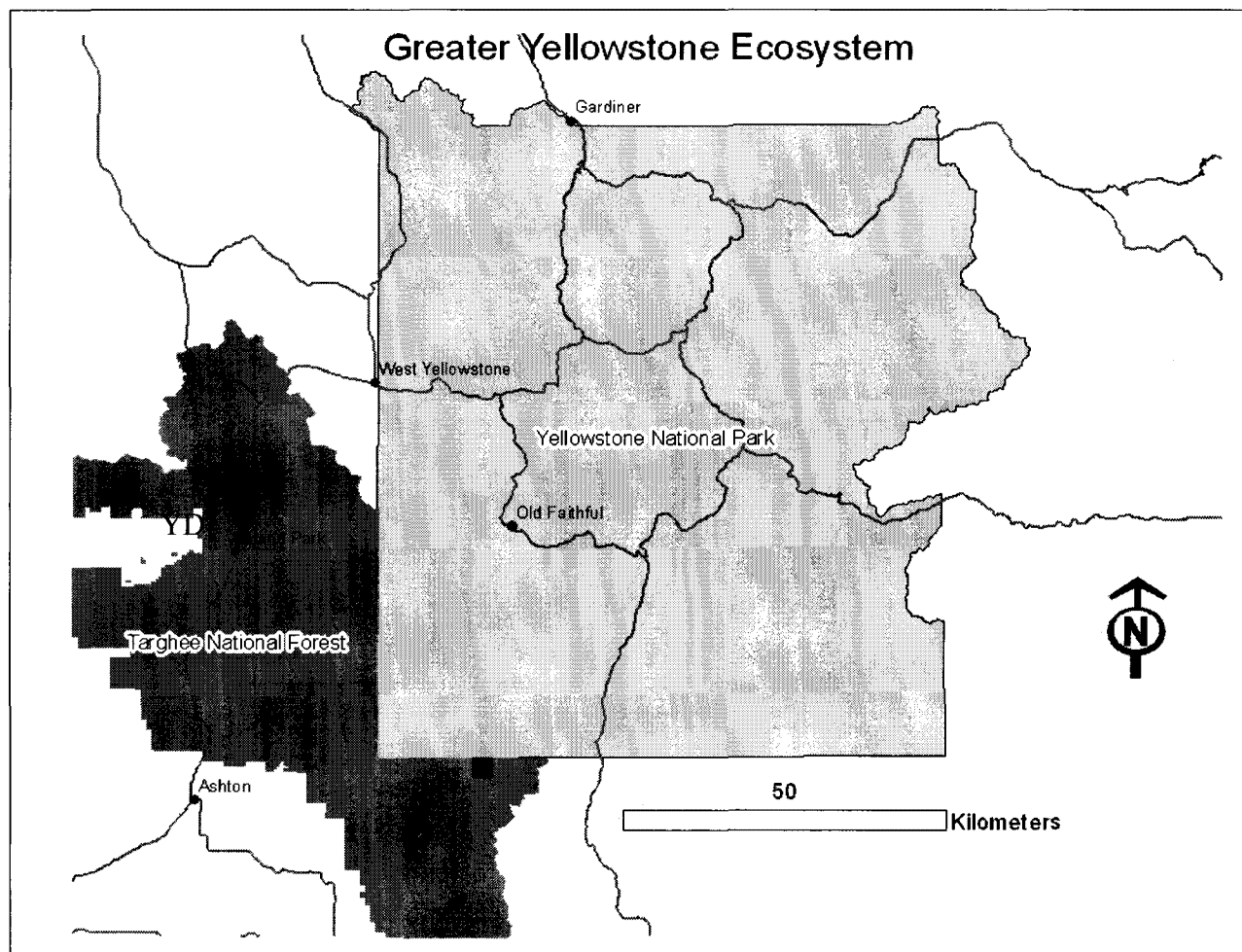


Figure 2. Comparison of biomass values among those directly measured by this study, those predicted by this study's allometric models, and those predicted by Comeau and Kimmins' allometric models.

Figure 2.

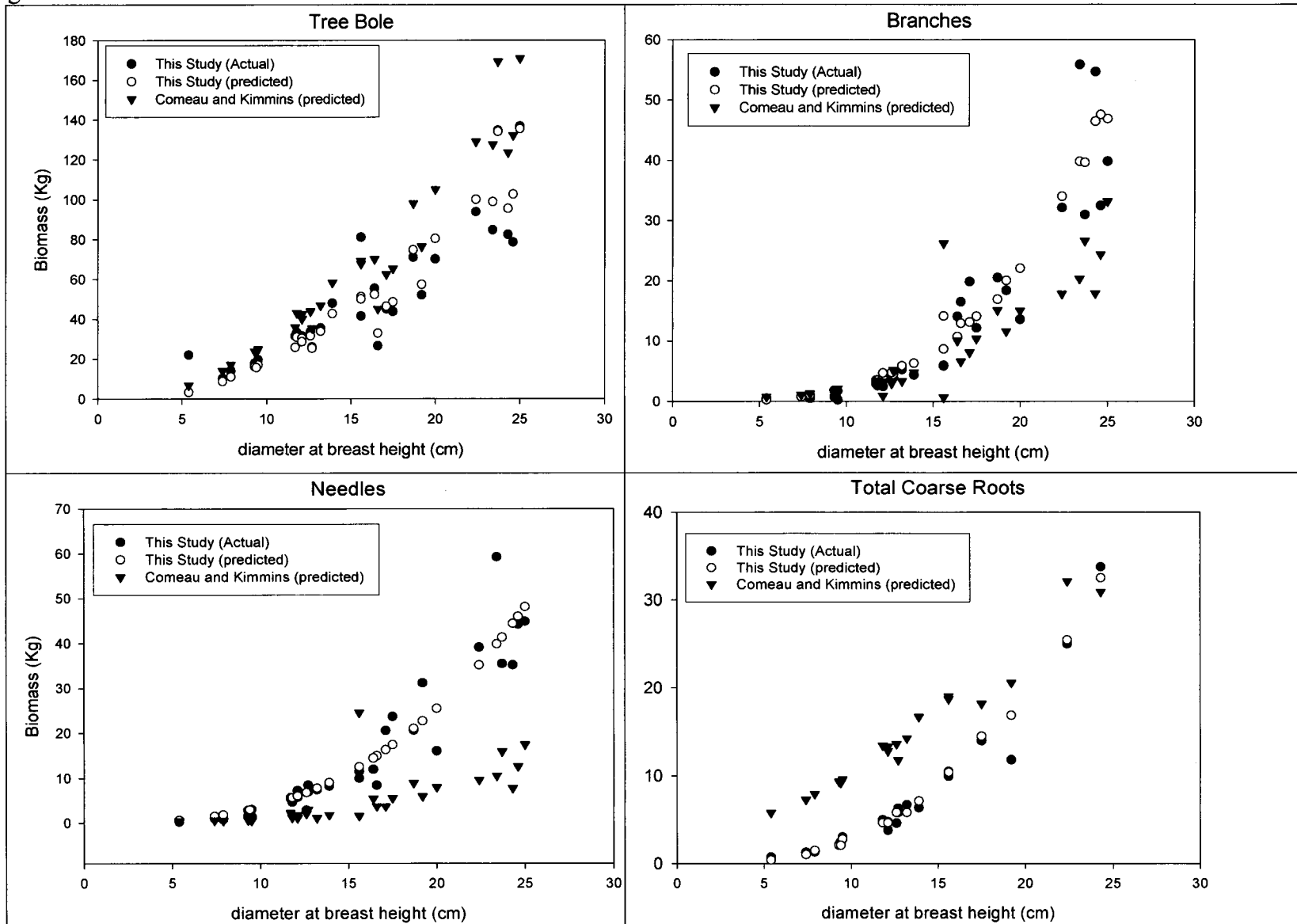


Figure 3. Comparison of biomass values among those directly measured by this study, those predicted by this study's allometric models, and those predicted by Pearson et al.'s allometric models.

Figure 3.

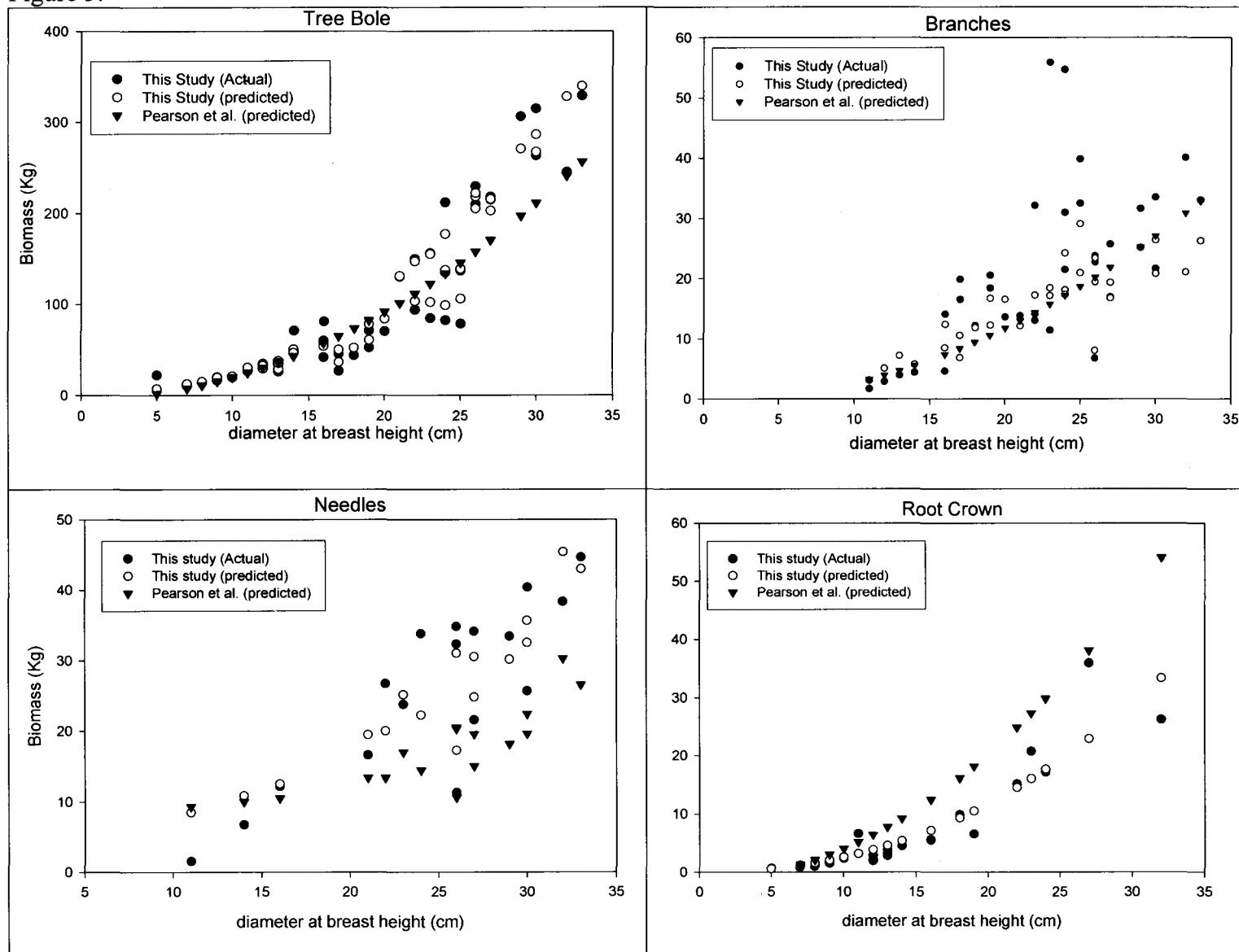


Figure 4: Biomass allocation patterns at the individual tree level for three *P. contorta* stands differing in densities and ages in the Greater Yellowstone Ecosystem. Different letters denote significance according to Tukey's HSD post-hoc analyses.

Figure 4:

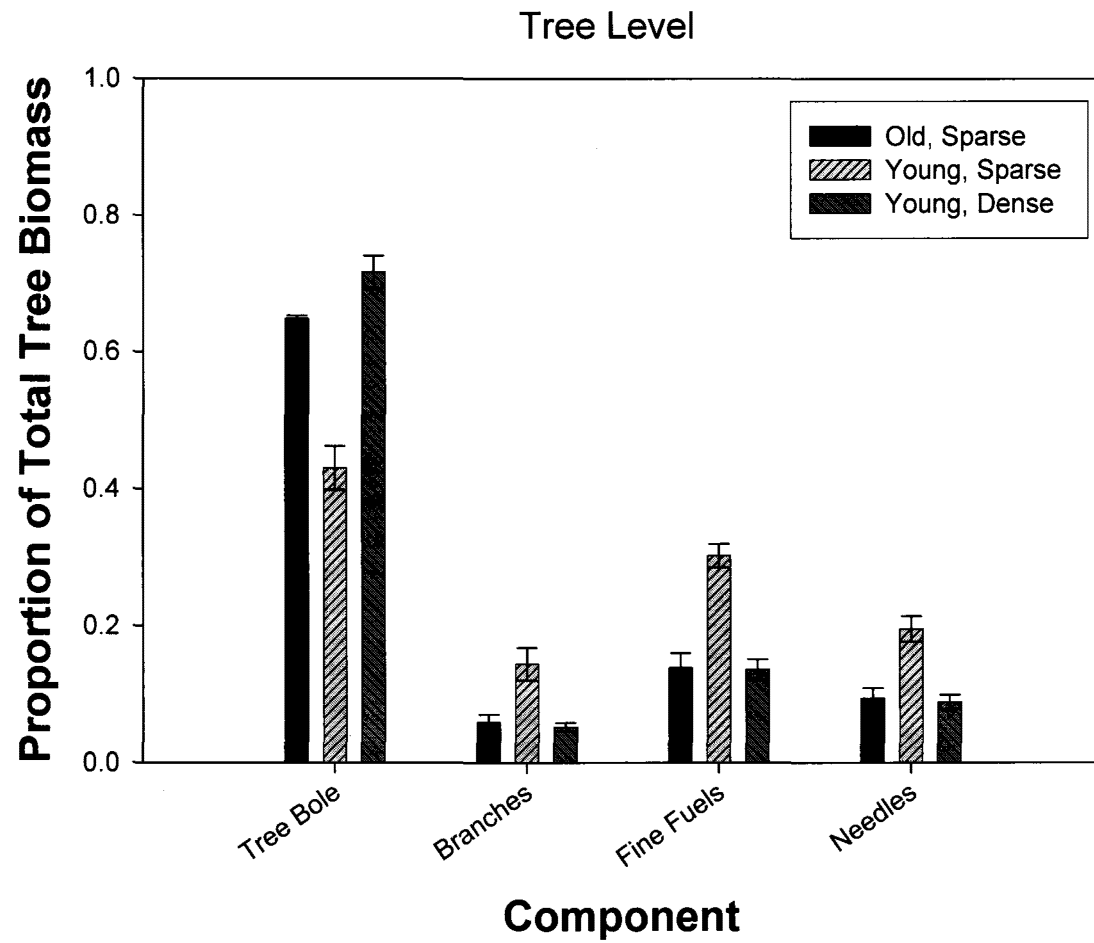
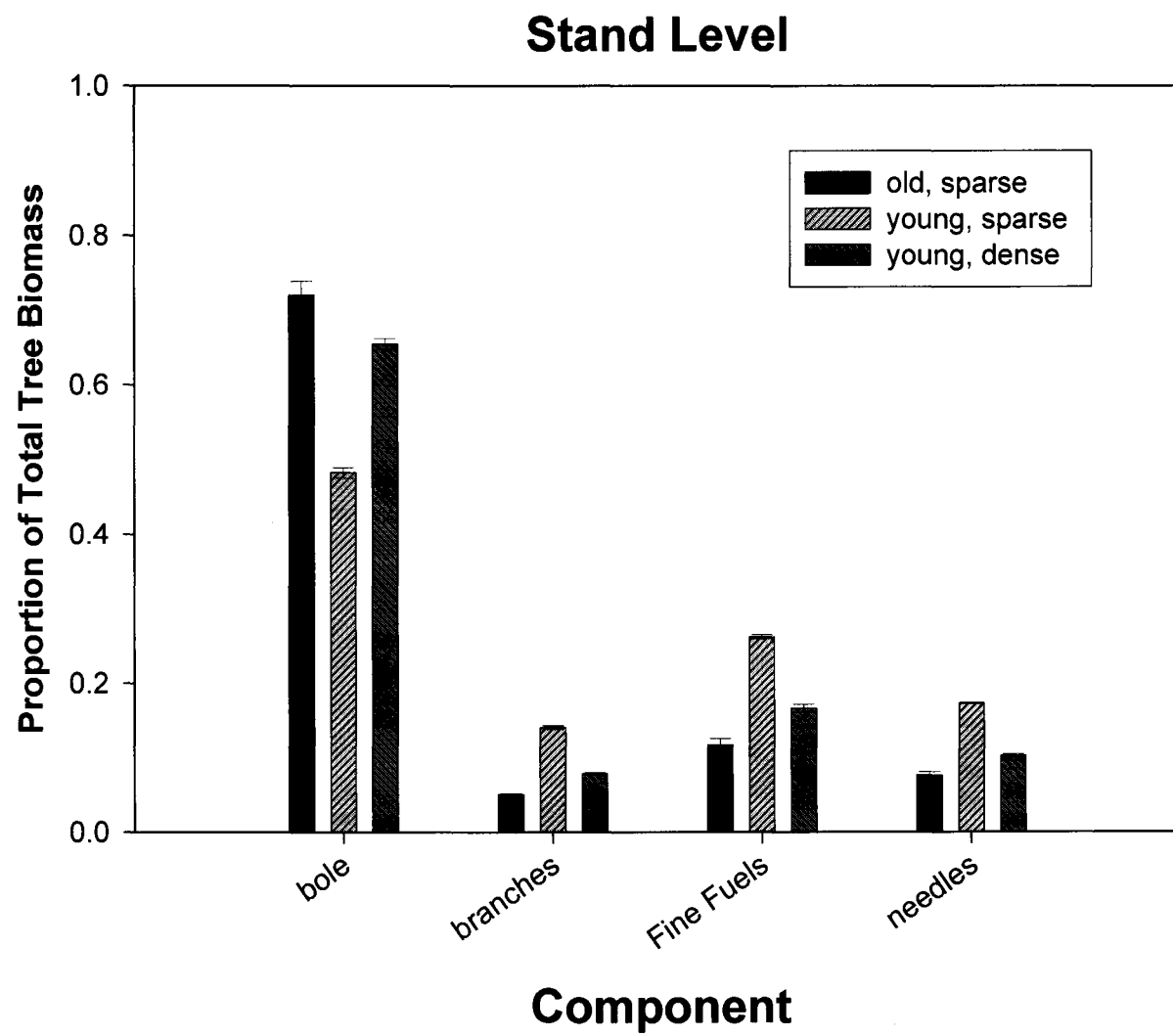


Figure 5: Biomass allocation patterns at stand level for three *P. contorta* stands differing in densities and ages in the Greater Yellowstone Ecosystem. Different letters denote significance according to Tukey's HSD post-hoc analyses.

Figure 5:



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